EXOTIC SPECIES OF CELTIS (CANNABACEAE) IN THE FLORA OF NORTH AMERICA

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ABSTRACT

Two species of *Celtis* are naturalized in North America. *Celtis australis* escapes locally in riparian woodland in the Sacramento Valley of northern California, while *C. sinensis* (new to the adventive flora of North America) escapes in a variety of habitats from widely separated sites in California and in the District of Columbia, with seedlings found up to 300 m from adult plants. Descriptions and illustrations of both species are provided.

RESUMEN

Dos especies de Celtis están naturalizadas en Norte América. Celtis australis escapa localmente en bosque riparios en el Valle de Sacramento del norte de California, mientras que C. sinensis (nueva para la flora adventicia de Norte América) escapa en una variedad de hábitats en sitios ampliamente separados en California y en el Distrito de Columbia, con plantas que se encuentran hasta a 300 m de las plantas adultas. Se aportan descripciones e ilustraciones de ambas especies.

The genus *Celtis* L. (Cannabaceae, traditional Ulmaceae; Sytsma et al. 2002) is a widespread group of ca. 60 or 70 species of trees and shrubs, about half growing in the north temperate zone. Several *Celtis* species are cultivated in North America. Most commonly cultivated are two native species, *Celtis occidentalis* L. (hackberry) and *C. laevigata* Willd. (sugarberry). Two exotic species, *C. australis* L. (native to the Mediterranean basin and southwest Asia; Browicz and Zieliński 1982; Tutin 1991; Zieliński 1979) and *C. sinensis* Pers. (native to China and Japan; Fu et al. 2004), are available in the nursery trade. Both are planted, primarily as street trees, mainly in warm interior valleys of California (Brenzel 2001). *Celtis sinensis* is occasionally planted in the eastern United States (Meyer et al. 1994; Dirr 1998), and is sometimes considered a species with potential for more widespread use as a landscape tree (Dirr 1998).

Native *Celtis* species are well known to be weedy in gardens and disturbed urban areas. The single report of *C. australis* escaping in Butte Co., California by Oswald (1994) is the only report of a non-native *Celtis* sp. reproducing outside of cultivation in North America. No exotic species of *Celtis* is treated in any continental or regional flora for North America (Barker 1997; Wilken 1993). However, Batianoff and Butler (2002) considered *Celtis sinensis* one of the worst invasive plants in south-east Queensland, Australia, where they found it capable of crowding out native vegetation and forming monocultures, suggesting that the species has the potential to become invasive in suitable conditions.

Herbarium specimens and field sites for *Celtis* were examined. Several field sites in California were confirmed for *C. australis* and *C. sinensis*. The latter was also found to escape in a single location in the District of Columbia.

Nesom (2000) suggests a simple, uniform terminology for describing the "reproductive status and dispersive success" of non-native species. Uniform treatment of invasives is certainly necessary to allow meaningful comparisons between different works. However, the simple categories Nesom suggests are often difficult to apply to newly escaping woody plants or other perennials with long generation times. Distinguishing between Nesom's categories of "waif" and "naturalized" depends on the scientists' estimate of the long-term reproductive behavior of the species in the habitat. This is often suitable for annuals or perennials that are short-lived or reproduce when young, but not suitable for woody plants, where it may be many years before the long-term ability of a population to persist and reproduce in the habitat can be estimated accurately—thus, before it can be known whether the population is naturalized. Unfortunately, the early

establishment phase is precisely the period when information about invasive tendencies of the species is most needed. It becomes important to document the habitats these species colonize and record their dispersal distances from seed sources. Invasive species have often gone unrecognized for long periods because they are not included in regional herbaria, floras, or other literature (Luken & Thieret 1995; Whittemore 2004). These two species are not described or illustrated in any North American flora (except McMinn & Maino 1947, who included *C. australis* as a cultivated species). A key, descriptions and illustrations are provided below to ensure that their populations can be recognized by local botanists.

TAXONOMIC TREATMENT

Identification of Celtis in North America is greatly complicated by unresolved taxonomic problems in a variable complex of shrubs and small trees, distributed over most of the United States, that are probably apomictic (Whittemore 2005a). These plants (referred to as the "small tree complex" below) are treated in different floras under a variety of names (the most commonly used, in the order they were first published, are Celtis pumila Pursh, C. tenuifolia Nutt., C. reticulata Torr., C. lindheimeri Engelm. ex K. Koch, and C. georgiana Small). None of the published treatments presents the variation in these plants adequately. Furthermore, of the five names listed above, only *C. pumila* and *C. reticulata* have been typified, and the correct application of the other names is in question. Until an adequate taxonomic treatment of this complex is available, it is not possible to write a full key to the North American species of Celtis. Furthermore, Celtis shows a very high level of within-plant leaf polymorphism, which greatly complicates identification. Leaves of juvenile or highly stressed plants are often very different from leaves of normal adults with the same genotype, and leaves of vigorous leaders may be much larger than leaves of fruiting laterals, and these two leaf types may differ very strongly in shape, especially in C. occidentalis and species of the small tree complex. Reliable identification of Celtis spp. may require studying fertile material, and comparing leaves that are subtending pedicels (Fernald 1950, Whittemore 2005b). The key below includes all Celtis species that grow outside of cultivation in the United States and Canada, but does not attempt to divide the small tree complex into natural taxa. For the taxonomy of Celtis subg. Mertensia (Kunth) Planch., see Berg and Dahlberg (2001).

| 1. | Stems with prominent nodal spines. Flowers in dense cymes, hermaphroditic flowers with many male flow- ers lower on the same cyme (branch scars visible on pedicel). Styles bisbifid (i.e. each lobe is again deeply |
|----|---|
| | divided) Celtis subg. Mertensia |
| | 2. Nodal spines straight. Leaves $1-3(-5) \times 0.4-2$ cm. Axils of basal veins with deeply invaginated domatia. |
| | Shrubs 2–6 m tall. Florida, Texas, New Mexico, Arizona Celtis ehrenbergiana |
| | (Klotzsch) Liebm. (=Celtis pallida Torr |
| | 2. Nodal spines curved. Leaves $5.5-10 \times 2.5-4$ cm (to 13×6 cm in the tropics). Axils of basal veins without |
| | domatia. Shrubs (often scandent) 5–12 m tall. Florida Celtis iguanea (Jacq.) Sarg |
| 1. | Stems unarmed. Hermaphroditic flowers solitary on axillary pedicels (without branch scars on pedicel). Styles |
| | bifid (i.e. with two undivided lobes) Celtis subg. Celtis |
| | 3. Abaxial surface of leaf uniformly pubescent over its whole surface, felty to the touch; leaf abruptly con- |
| | tracted to a slender acumen, each margin with 20–32 teeth Celtis australis |
| | 3. Not as above: either abaxial surface of leaf with hairs confined to veins and vein axils, smooth to the touch, |
| | or the leaf blade evenly tapered or gradually narrowed to the slender acumen and entire or with no more |
| | than 16 teeth on each side. |
| | 4. Large shrubs or small trees to 12 m tall, with leaning trunks and horizontal or arching leaders or (with |
| | age) multiple spreading trunks. Pollen largely or entirely aborted, seldom more than 10% of the grains |
| | stainable with acetocarmine, stainable grains (if present) very variable in size and number of pores, or |
| | else anthers remaining small and indehiscent. "Small tree complex" |
| | 4. Excurrent trees to 30 m tall, typically with one strong vertical trunk (occasionally 2 or 3 parallel upright |
| | trunks), if small then with erect leaders. Anthers always dehiscent, pollen grains uniform in size, uniformly |
| | 3-porate, 95–100% stainable with acetocarmine. |
| | 5. Leaves subtending pedicels ovate to ovate-elliptic, acute or short-acuminate, basal secondary veins |
| | extending (0.5–)0.6–0.75 length of blade; bark without corky outgrowths Celtis sinensis |
| | 5. Leaves subtending pedicels lanceolate, obliquely triangular or triangular-ovate, acuminate (usually |

slenderly so), basal secondary veins extending 0.3–0.55 length of blade; bark with prominent corky

warts and ridges.

- 6. Leaves generally bright green on both surfaces; leaves subtending pedicels evenly tapering or gradually narrowed to the slender acumen; leaves of vigorous leaders larger but similar in shape; mature drupes 6–8 mm in diameter, brownish-orange or red ______ Celtis laevigata Willd.
- 6. Leaves generally paler abaxially; leaves subtending pedicels abruptly narrowed to the acumen; leaves of vigorous leaders larger and different in shape (often lanceolate or oblong, apex acute or short-acuminate, base often shallowly cordate); mature drupes 8–11 mm in diameter, dark brownish purple or purplish red (but immature drupes may be red or orange) _____Celtis occidentalis L.

Celtis australis L., Sp. Pl. 1043. 1753. (Fig. 1a).

Deciduous trees to 20(–25) m tall. Bark gray, smooth or finely roughened. Branchlets brown or purplish, pubescent with spreading hairs to 0.5 mm long. Winter buds brown or purplish, 3–5 mm long, puberulent. Stipules linear or lanceolate, 3–6 mm, pubescent, fugacious. Leaves subtending pedicels with petiole 9–17 mm, tan, pubescent, dorsal sulcus usually a narrow sharp groove, seldom broad and shallow; leaf blade narrowly elliptical to lanceolate or lance-ovate, 8–11 × 3–5 cm, rather thick but flexible, adaxial surface dull dark green, abaxial surface light green or glaucous, pubescent with spreading hairs over veins and whole blade, felty to the touch; secondary veins 2–4 on each side, basal secondary veins extending (0.45–)0.5–0.7 length of blade; base cuneate to rounded, usually strongly asymmetrical, margin serrate from base to apex with sharp teeth 2–3 mm long, teeth 20–32 on each side; leaf apex abruptly contracted to a slender acumen; leaves of sterile leaders similar but often larger, to 16 cm long. Male flowers fascicled in axils of bud-scales and lower leaves, bisexual flowers solitary in lower leaf axils, reaching anthesis as leaves emerge in the spring. Pollen not seen. Drupes 1 per leaf axil, pedicel pubescent (at least proximally), 19–31 mm long, 1.6–2.7 times as long as subtending petiole. Drupe subglobose to pyriform, usually tapering to style-base, 10–12 mm in diameter, very dark brown (almost black) at maturity.

Distribution and Flowering.—Found in North America in riparian woodland, elev. 15–60 m. Flowering as leaves emerge in the spring; fruiting mid- to late fall.

Feral North American specimens examined. **U.S.A. California. Butte Co.:** spontaneous in riparian *Quercus lobata - Platanus* forest, Lower Bidwell Park between the nature center and Chico Creek, 39° 45' N, 121° 49' W, *A.T. Whittemore 06-004* (NA, UC). Tree ca. 8 m tall, edge of undeveloped woodland 10 m S of footbridge at W edge of golf course, Upper Bidwell Park, Chico, *V. Oswald 417* (CHSC). **Yolo Co.:** Spontaneous trees in dense secondary woods on banks of waterway (formerly a tributary of Willow Slough but now an artificial channel that drains north into the Willow Slough Bypass) just east of F street near jct. Faro Ave., 38° 34' N, 121° 44' W, *A.T. Whittemore 06-010* (NA, UC).

Celtis australis can be recognized by its smooth or finely roughened bark (not developing corky warts or ridges like the native North American species), its leaf blades that are sharply serrate and very slenderly long-acuminate from a narrowly elliptical to lanceolate or lance-ovate body and uniformly felty-pubescent beneath, and its large, dark brown or black drupes (the drupes ripen orange-brown, red or purplish in other American species).

Celtis australis was reported by Oswald (1994) as an escape in Bidwell Park, Chico, California. This site was visited in August 2006. The road between the site of the former Forestry Station and the current Nature Center is lined with large, well-established trees, evidently planted many years ago and now fruiting heavily. Seedlings and saplings are common in the vicinity of these trees. The majority are found in disturbed roadside habitats, but well-established small trees are also found in open *Quercus lobata - Platanus* woodland in the vicinity of the planted trees. Some of these trees are fruiting in this habitat, so *C. australis* is definitely established in native habitats and should be considered locally naturalized.

Feral plants of *Celtis australis* were also found along a waterway on the north side of Davis, in dense secondary forest that grew up on disturbed soil exposed when the waterway was channelized approximately thirty years ago. No cultivated trees were seen nearby, but the storm-drain system from much of Davis empties into this waterway, so seeds could easily have washed in from elsewhere in Davis (where *C. australis* is occasionally planted as a street tree). The land is not under cultivation, so under a strict application of the definitions of Nesom (2000) these trees are either waifs or naturalized (depending on their ultimate ability to reproduce themselves locally), but the site was heavily disturbed during the channelization, and it receives

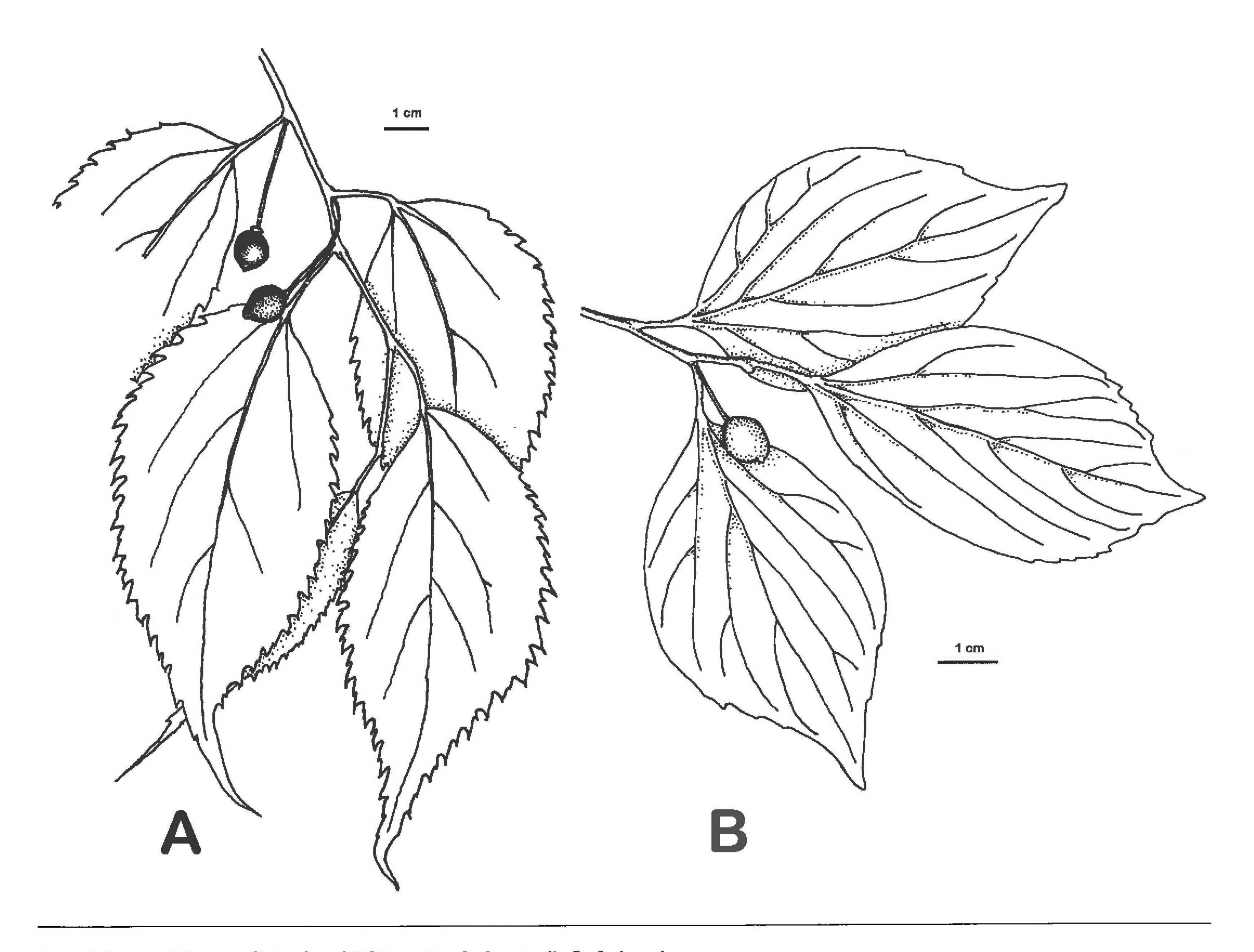


Fig. 1. Foliage and drupes of introduced Celtis species. A. C. australis. B. C. sinensis.

extra water from urban runoff, so it might be more realistic to regard them as weedy rather than invasive. The site is worth noting, however, as it does suggest that *C. australis* is capable of dispersing over significant distances.

Celtis sinensis Pers., Syn. Pl. 1:292. 1805. (Fig. 1b).

Deciduous trees to 20 m tall. Bark gray, smooth or finely roughened. Branchlets brown, brown-pubescent, sometimes becoming glabrescent late in season. Winter buds dark brown, 1-3 mm long, glabrous or puberulent. Stipules linear or lanceolate, 3-5 mm, pubescent, fugacious. Leaves subtending pedicels with petiole 3-10 mm, brown, pubescent, dorsal sulcus broad and shallow; leaf blade ovate to ovate-elliptic, $3-10 \times 3.5-6$ cm, rather thick but flexible, adaxial surface glossy dark green, abaxial surface light green, usually inconspicuously yellowish-brown puberulent when young, at maturity with hairs abaxially scattered on major veins and sometimes tufted in vein axils, smooth to touch, secondary veins 3-4 on each side, basal secondary veins extending (0.5-)0.6-0.75 length of blade; base rounded, obtuse, or obliquely truncate, subsymmetrical to moderately oblique, margin subentire to crenate on apical half, teeth 0-16 on each side, apex acute or short-acuminate; leaves of sterile leaders similar but often larger, to 9 cm long. Male flowers fascicled in axils of bud-scales and lower leaves, bisexual flowers solitary in lower leaf axils, reaching anthesis as leaves emerge in the spring. Anthers dehiscent, pollen grains uniform in size, uniformly 3-porate, 97-99% stainable with acetocarmine. Drupes 1(-3) per leaf axil, pedicel rather stout, pubescent (at least proximally), 4-10 mm long, 1-1.5 times as long as subtending petiole. Drupe subglobose, 5-7(-8) mm in diameter, brownish orange at maturity.

Distribution and Flowering.—Found in North America in riparian woodland, dry grassland, open woodland margins, elev. 15–580 m. Flowering as leaves emerge in the spring; fruits ripe mid- to late fall.

Feral North American specimens examined. **U.S.A.** California. Butte Co.: Occasional tree on E edge of Dry Creek in riparian woodland among sycamores, alders and willows, ca. 0.5 km N of jct. Pentz and Mesilla Valley Rds., elev. ca. 120 m, *B. Castro* 436 (CHSC). **Orange Co.:** Weed tree invading UC Irvine Arboretum, UCI campus near intersection of Jamboree Blvd. and Campus Dr., elev. 15 m, *A.C. Sanders* 27326 (UCR). **San Bernardino Co.:** Spontaneous in alder forest in canyon, Arrowhead Hot Springs and immediate vicinity; Coldwater Canyon and Strawberry Creek Canyon, ca. 0.5 mi E of the old Arrowhead Hot Springs Hotel, San Bernardino Mtns., elev. 580 m, *A.C. Sanders* 13812 (UCR). **Yolo Co.:** Spontaneous trees to 5 m tall in dense secondary woods on banks of waterway (formerly a tributary of Willow Slough but now an artificial channel that drains north into the Willow Slough Bypass) just east of F street near jct. Faro Ave., 38° 34' N, 121° 45' W, *A.T. Whittemore* 06-011 (NA, UC). Spontaneous tree 6 m tall in disturbed alkali grassland between road 101A and the railroad tracks, 0.6 km south of Road 29, north side of Davis, 38° 35' N, 121° 45' W, *A.T. Whittemore* 06-012 (NA, UC). **District of Columbia:** Disturbed woodland margins, service road to Administration and Bonsai Pavilion loading docks, United States National Arboretum, 38° 55' N, 76° 58' N, *A.T. Whittemore* 04-012 (NA). Disturbed woodland margins near Administration Building parking lot, United States National Arboretum, 38° 55' N, 76° 58' N, *A.T. Whittemore* 04-016 (NA).

Celtis sinensis can be recognized by its smooth bark, its rather leathery, glossy leaves, with the margins usually crenate or bluntly serrate and the apex often rounded-acute.

Celtis sinensis has never been reported to escape in North America, but field sites and herbarium specimens were found documenting feral populations over a surprisingly wide geographic range and in a variety of habitats. It is not common at any of the sites and there is currently no evidence that it can be an aggressive competitor in our flora (as reported for Australia; Batianoff and Butler 2002), but saplings are often found several hundred meters from possible seed sources, suggesting that effective dispersal agents for this species exist in North America. On the grounds of the U.S. National Arboretum in Washington DC, young trees are occasionally found in open margins of native deciduous forest, often 100-300 m from the nearest possible seed source, but feral plants have not been observed in closed forest (except as a weed in cultivated beds). The Butte County site (Castro 436) is riparian woodland in dry, grassy low foothills of the northern Sierra Nevada, and according to the herbarium label, the feral plants are ca. 200 m from planted trees of C. sinensis. The tree near Road 101A in Yolo County (Whittemore 06-012) is in native alkali grassland that has never been cultivated but has probably been subject to some disturbance because of its proximity to the county road and railroad. This tree is at least 300 m from the nearest possible seed source. The long dispersal distances seen at most of the sites are not surprising, since the sweet, fleshy drupes are well suited to bird dispersal. Fleshy bird-dispersed fruit has been shown to be a significant predictor of invasive behavior in woody plants (Widrlechner et al. 2004), so further tracking of this species is desirable.

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